

# THE BASES OF ANGIOSPERM PHYLOGENY: PALEOBOTANY<sup>1</sup>

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## ABSTRACT

Analysis of certain fossils that have been used as evidence for a pre-Cretaceous origin and diversification of the angiosperms indicates that these fossils are non-angiospermous. A review of the sequential development of morphological features exhibited by Early Cretaceous pollen and leaves indicates that the initial radiation of the angiosperms was occurring at that time. The monocotyledons and dicotyledons diverged early before either class attained a moderate degree of diversity. Subclass Magnoliidae has retained the morphological grade exhibited by the earliest dicotyledonous pollen and leaves. The next youngest grade of Early Cretaceous pollen is found in putatively primitive members of Hamamelididae and Ranunculidae. Stratigraphic series of Early Cretaceous foliage indicate a transition from the morphological grade of Magnoliales to leaf morphology characteristic of Rosidae. Late Cretaceous wood assemblages are characterized by a preponderance of anatomical features that have been previously postulated as primitive and typically lack features thought to be advanced.

Twenty years ago, the inclusion of paleobotany in a symposium of this nature would have been little more than a token gesture. The then prevalent concept was that by the Cretaceous—the time of their first entry in significant numbers in the fossil record—the angiosperms were well diversified into extant orders and families, and even genera (Axelrod, 1970). The diversification having taken place in some area remote from basins of deposition and fossilization (e.g., tropical uplands or Malesia), paleobotany would provide almost no evidence bearing on the phyletic relationships between major angiosperm groupings.

During the last twenty years, however, a growing body of evidence has indicated that the angiosperms were undergoing their major evolutionary radiation during the Cretaceous (Fig. 1). The lack of any definite angiosperm pollen in a great array of pre-Cretaceous samples led Scott et al. (1960) and Hughes (1961) to question the supposed great antiquity of angiosperm diversification. More significantly, palynological work on Cretaceous sequences has uniformly shown that, from the level of the first known and morphologically simple angiosperm pollen types, successively younger horizons yield successively more complex and

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diverse arrays of pollen (Doyle, 1969a; Muller, 1970). Although Early Cretaceous angiosperm leaves have typically been matched with leaves of extant genera and families, renewed interest in foliar morphology of both extant and fossil angiosperms has indicated that Early Cretaceous sequences of angiosperm leaves also display the attainment of increasingly higher levels of specialization (Doyle & Hickey, 1972; Hickey & Doyle, 1972), and that many of these earliest leaves represent the same morphological grade as putatively primitive extant angiosperms (Wolfe, 1972).

We thus consider that paleobotany can contribute to an understanding of phyletic relationships between major angiosperm groups. The overwhelming bulk of angiosperm fossils, of course, represent organs that have not been the primary basis of angiosperm classification and speculation on phylogenetic relationships, that is, much of angiosperm history must be deciphered from interpretations of pollen, leaves, and wood rather than flowers. Basic to such interpretations are the correlations that can be made between morphological specializations in these organs and taxonomic position in systems of classification. As papers presented in this symposium indicate (Hickey & Wolfe; Walker & Doyle), such correlations can be made. Moreover, as classifications become more broadly based on all aspects of the plant, such classifications will be easier to evaluate by means of paleobotanical evidence.

Paleobotanists can approach this problem of correlation of morphological specialization with taxonomic position in two basically dissimilar ways. The first is to attempt to find, for each given fossil, a modern plant that is morphologically similar. If, however, the significance of the observed similarities as indicators of phylogenetic relationships of the modern plant is not understood, then we clearly could be analogizing. Until recently, almost all work on angiosperm fossils used such an approach. If meticulously carried out, such an approach will perhaps give some idea as to the oldest occurrence of a given extant genus and low-level suprageneric groupings, but this approach is basically incapable, as Stebbins (1950) pointed out years ago, of recognizing extinct groups intermediate between various major groups represented in the extant flora.

The second approach to paleobotany can be initially independent of comparisons of fossils with extant plants. In given stratigraphic sequences evolutionary series can be postulated, based on a trend from one morphological type to another. This trend in a time dimension allows us to infer which morphological type is ancestral (oldest) and which is derived (youngest). If such character phylogenies are integrated with the comparative morphological data from extant angiosperms, then we are in a position to evaluate systems of classification that have attempted to incorporate concepts of phylogeny. We are also capable of recognizing which fossils represent extinct intermediates and even fossils that represent distinct evolutionary branches that have failed to survive.

Paleobotany, moreover, is a prime tool in uncovering convergences and hence determining whether groups are mono- or polyphyletic. If a particular character or set of characters in a given organ can be demonstrated to have evolved in more than one temporal-morphological series, then clearly two taxa that possess that character or character set are not necessarily phylogenetically related. If a



particular character can be shown to have evolved in only one series, then extant plants possessing that character compose a monophyletic group or clade.

#### EVIDENCE ON PRE-CRETACEOUS DIVERSIFICATION

A widely held concept, as we stated previously, is that the angiosperms originated in the early Mesozoic or even late Paleozoic and, by the time they entered the fossil record in significant numbers in the Aptian-Albian interval, had undergone their basic diversification into various extant orders and even families (e.g., Axelrod, 1970). Cited as proof for this concept are various early putative angiosperms. It is pointless to discuss certain of these occurrences; some of them, such as the leaves called *Ungeria* and *Propalmophyllum*, are so poorly preserved that groups such as the ferns or gymnosperms could be represented. Other occurrences of early angiosperms, such as the putatively Jurassic palm wood and roots from Utah (Tidwell et al., 1970), have proven to be almost certainly of Tertiary age (Scott et al., 1972). Still other occurrences, such as the pollen called *Eucommiidites*, have been demonstrated to be gymnospermous rather than angiospermous (Hughes, 1961). Read & Hickey (1972) have shown that *Sanmiguelia*, a palm-like Triassic leaf, lacks features definitive of the palms, and Doyle (1973) has further demonstrated that *Sanmiguelia* lacks diagnostic features of the monocotyledons as a whole.

We will discuss two other examples: the late Triassic leaf called *Furcula* and the Hauterivian fructification called *Onoana*. These two examples, we think, illustrate various problems relative to the taxonomic placement of fossils.

Harris (1932), the describer of the leaf *Furcula*, suggested a possible angiospermous affinity based on the character of the stomatal apparatus and the reticulate or net venation. The stomatal apparatus is indeed the syndetocheilic type that is of wide occurrence in the angiosperms, but in itself is an insufficient basis for assignment to the angiosperms because the same type also occurs in gymnosperms such as the Cycadeoidales and Gnetales. Investigators have, however, overlooked one critical feature of the net venation of *Furcula*. In the woody dicotyledons, with which *Furcula* is compared, the secondary venation is a fundamentally closed type; the closure is most typically accomplished by the looping of the secondary veins, but is also in some instances accomplished by strong branches of the secondary veins or by a marginal vein. Harris noted, however, that in *Furcula* the secondary veins and branches ended blindly at the margin of the lamina and that a continuous marginal vein was lacking; this is a decidedly non-dicotyledonous characteristic and basically represents a modified open venation system. Further, Harris noted that *Furcula* had another feature commonly found in pteridospermous gymnosperms, a bifurcating lamina. Although it is possible that *Furcula* represents some gymnospermous sister-group to the angiosperms, it clearly is not angiospermous.

The oldest fossil interpreted as an angiospermous fruit is *Onoana* from the Hauterivian of California (Chandler & Axelrod, 1961); this fructification thus predates the first occurrence of any other angiospermous organ. *Onoana*, however, does not display any characteristics confined to the angiosperms, that is, it cannot be determined whether *Onoana* is a seed or a fruit; the angiospermous affinity



rests entirely on picture-matching comparisons to fruits of Icacinaceae, particularly the extinct genus *Stizocarya*. In Icacinaceae, the endocarp is pierced partially by canals and is typically formed of interdigitating cells lacking definite orientation; when present, an inner layer is composed typically of interlocking cells, and, in the instance of *Stizocarya*, these cells are star-shaped (Reid & Chandler, 1933). Although *Onoana* has canals in what is interpreted as the endocarp, this layer is formed of apparently parenchymatous cells that are radially aligned; the inner layer in *Onoana* is formed of transversely aligned cells. Thus, the layers that are supposedly homologous between *Onoana* and Icacinaceae are in *Onoana* atypical for Icacinaceae. Added to this is the fact that pitted Icacinaceae have canals that are oriented radially, but in *Onoana* the canals range from radially to obliquely oriented. Thus, in several features, *Onoana* differs from typical icacinaceous fruits; if the relationship to Icacinaceae is problematic, then so is the relationship to the angiosperms because the latter relationship is based on the former. We consider it equally plausible that the inner layer of *Onoana* is homologous with the typically collapsed fleshy inner integumentary layer of gymnosperms and that the supposedly parenchymatous layer may in fact be sclerenchymatous as in gymnosperms, which is indicated by the presence of some fibers near the outer part of this layer. Clearly, it has not been established whether *Onoana* is angiospermous or gymnospermous, but the lack of definitive angiospermous features makes it an insecure basis for inferring the time of diversification of the angiosperms.

Even less secure is the determination of the modern icacinaceous genus *Phytocrene* from Cenomanian or Turonian beds of New York. The object attributed to this genus by Scott & Barghoorn (1957) is apparently not anatomically preserved, and the determination rests solely on the presence of external pits in the fossils. Reid & Chandler (1933: 322) noted that all endocarps of extant Icacinaceae are bisymmetric but the New York specimens are, at best, irregularly bisymmetric to subtriangular. We do not think that sufficient evidence has been presented to substantiate the determination of the New York material as Icacinaceae or even as angiospermous.

We thus consider that there is no unequivocal evidence that indicates a pre-Cretaceous origin for the angiosperms. The supposed diversity of early angiosperm leaf floras is, as discussed elsewhere (Wolfe, 1973), a logical artifact of attempting to match fossil and modern leaves without any concept as to the phyletic and taxonomic significance of various similarities and dissimilarities. As we argue below, the known fossil record of Cretaceous angiosperms can best be interpreted to indicate that the angiosperms were undergoing diversification at major taxonomic levels and that continuing investigations of Cretaceous angiosperm fossils will provide many answers to phylogenetic problems.

## THE CRETACEOUS RECORD

### POLLEN

One of the most intensively studied Cretaceous sections bearing on the early stages of angiosperm evolution consists of the Potomac Group and Raritan Formation of the Atlantic Coastal Plain (Brenner, 1963, 1967; Doyle, 1969a,



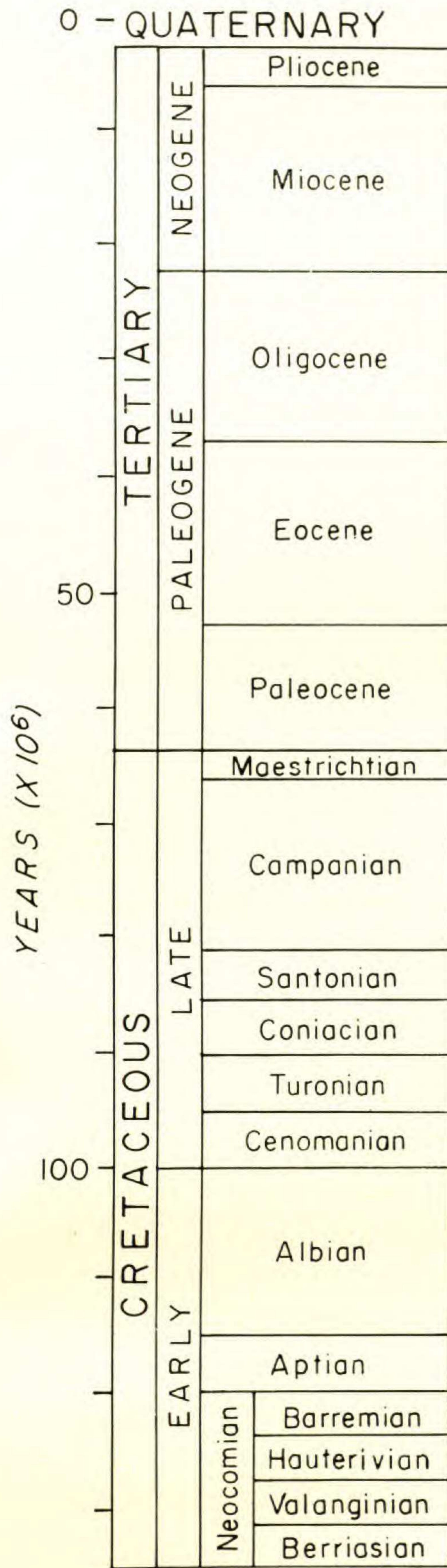


FIGURE 1. Approximate duration of Cretaceous stages and Tertiary epochs (from Wolfe, 1973).



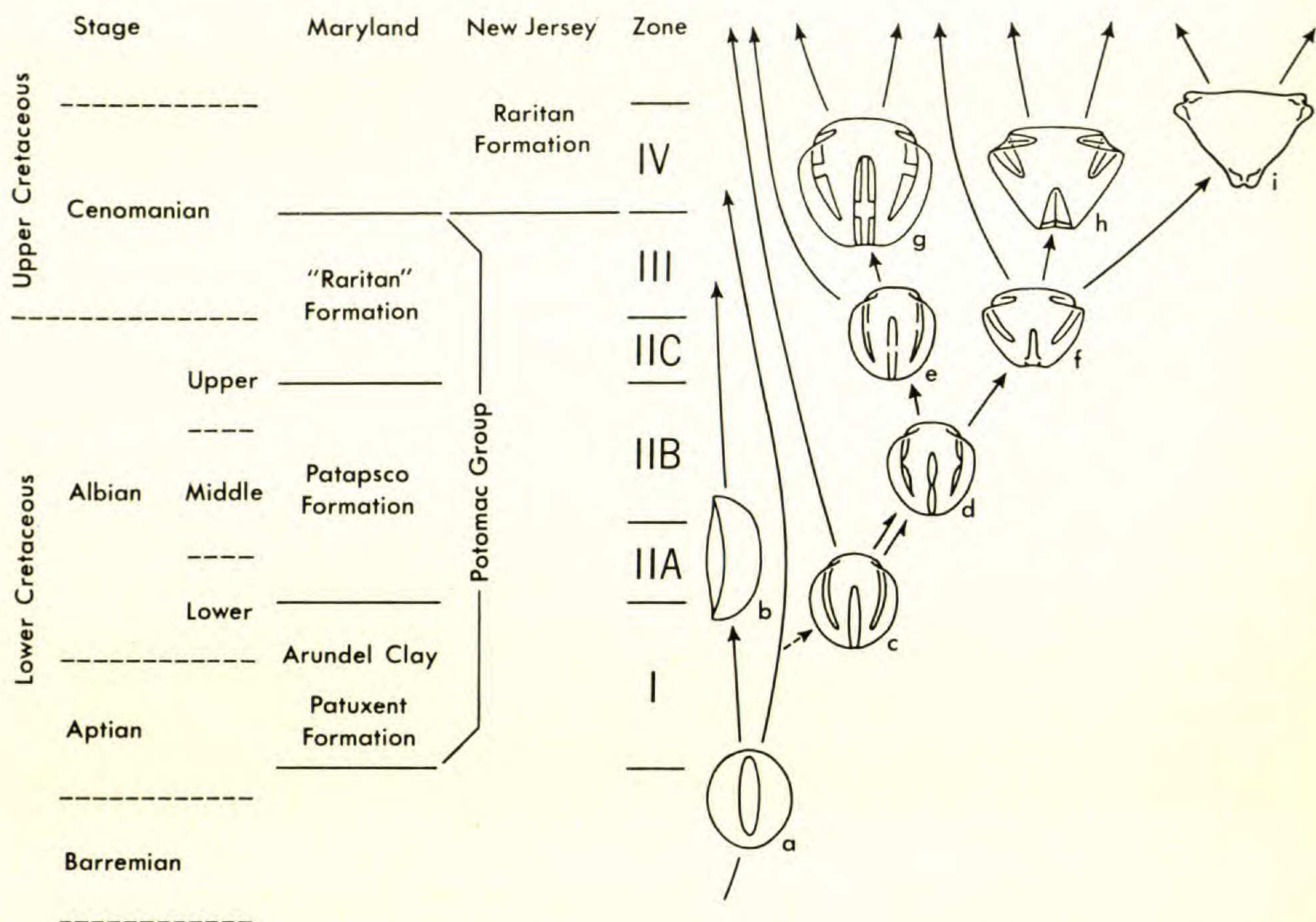


FIGURE 2. Stratigraphic subdivisions of the Atlantic Coastal Plain mid-Cretaceous section, and stratigraphic distribution and presumed evolutionary relationships of major angiosperm pollen types (modified from Doyle, 1973). Suggested correlations of the Maryland and New Jersey lithological units (formations) with the standard European stage sequence are indicated to the left; informal biostratigraphic units or pollen zones (Brenner, 1963; Doyle, 1969b, 1973; Doyle & Hickey, 1972) are indicated by roman numerals in the middle. Pollen types indicated to the right are: (a) generalized tectate-columellate angiospermous monosulcates (*Clavatipollenites*, *Retimonocolpites* spp.); (b) monocotyledonoid reticulate monosulcates (*Liliacidites* spp.); (c) generally reticulate-tectate tricolpates (non-magnoliid dicotyledons: *Tricolpites* spp.); (d) generally reticulate-tectate tricolporoidates (*Tricolpites*, *Tricolporoidites* spp.); (e) small, generally smooth-walled, prolate tricolporoidates (*Tricolporoidites* spp.); (f) small, generally smooth-walled, oblate-triangular tricolporoidates (*Tricolporoidites*, *Perucipollis* spp.); (g) larger, often more highly sculptured, prolate tricolpor(oid)ates (*Tricolporoidites*, *Tricolporopollenites* spp.); (h) larger, often more highly sculptured, oblate-triangular tricolpor(oid)ates (*Tricolporoidites*, *Tricolporopollenites* spp.); (i) primitive members of the triporate Normapolles complex (*Complexiopollis*, *Atlantopollis* spp.). Arrows indicate modes of origin, not necessarily individual evolutionary lines. The dashed arrow indicates the uncertain mode of origin of tricolpates; the double arrow emphasizes the multiple origin of tricolporoidates from tricolpates.

1969b, 1970, 1973; Wolfe & Pakiser, 1971). Although only the middle part of the Raritan Formation is dated directly by marine fossils, close similarities with pollen and leaf floras of other areas which have been dated independently allow detailed correlations with the standard European stage sequence (Fig. 1; cf. Brenner, 1963; Kemp, 1968, 1970; Norris, 1967; Hedlund & Norris, 1968; Doyle, 1969a, 1969b; Doyle & Hickey, 1972, in press; Wolfe & Pakiser, 1971; Pacltová, 1971). These comparisons also indicate that the pattern of diversification of pollen types seen in the Potomac-Raritan section (summarized on right side of Fig. 2) is sufficiently consistent with changes occurring elsewhere in the world to serve



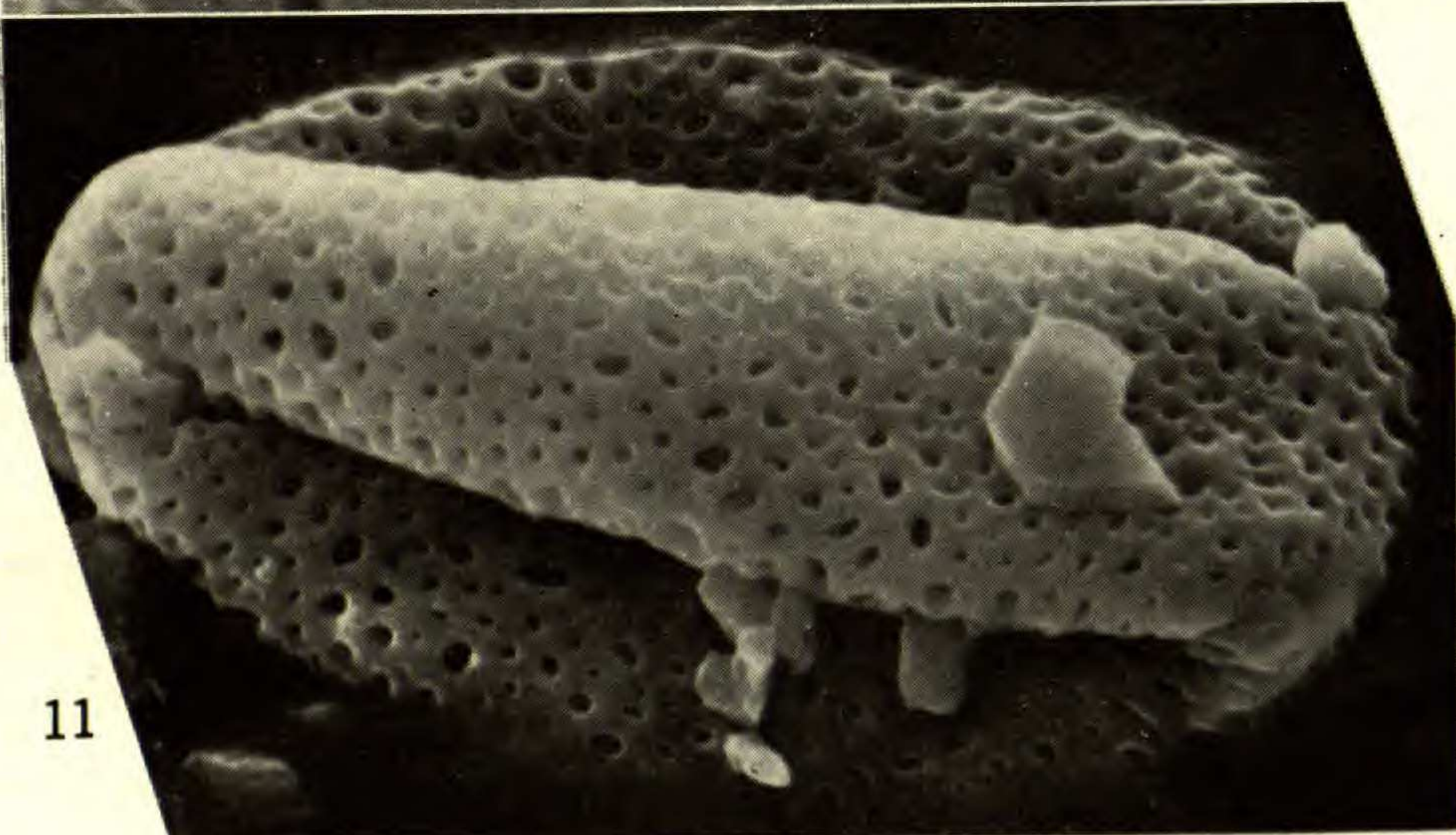
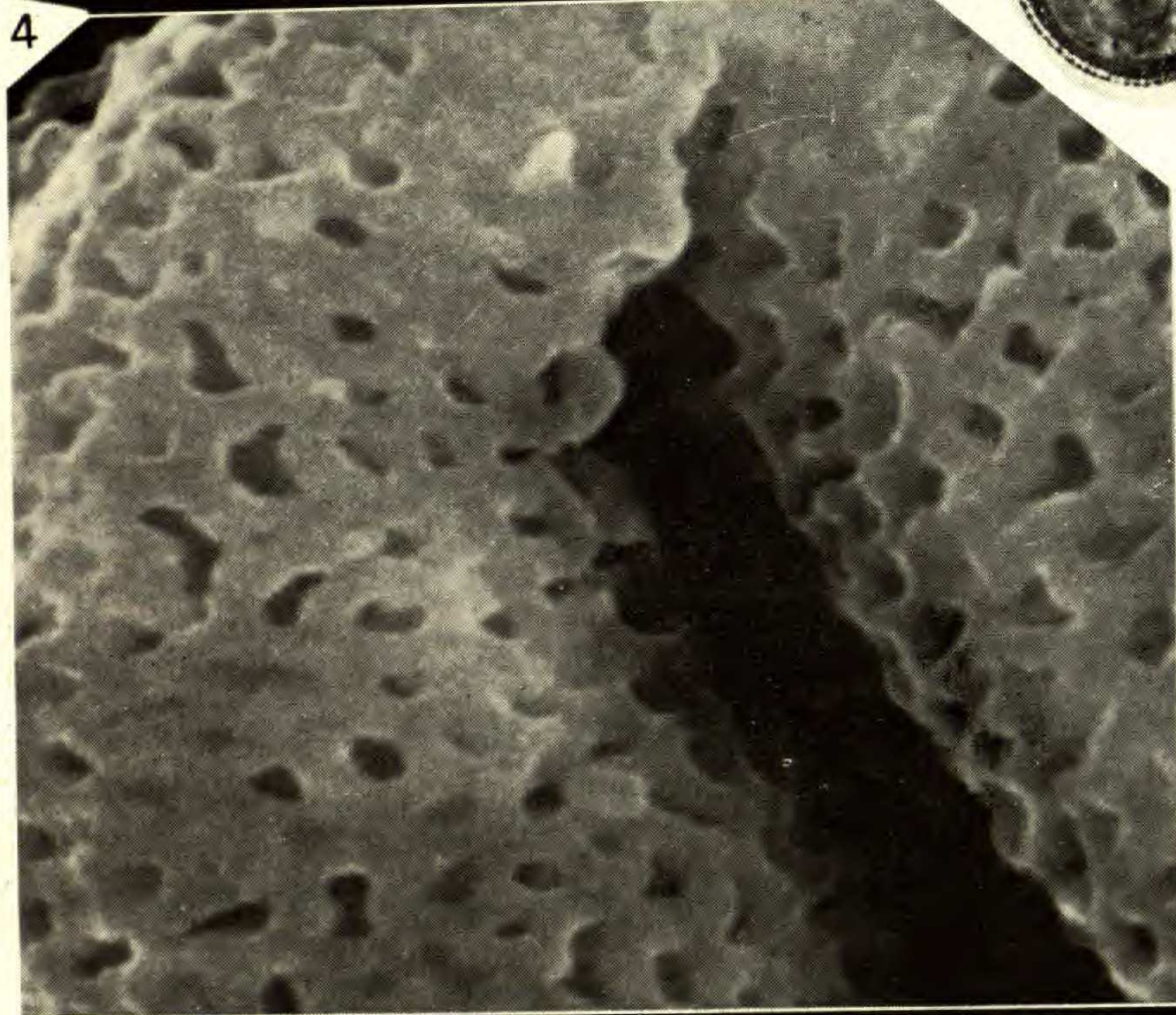
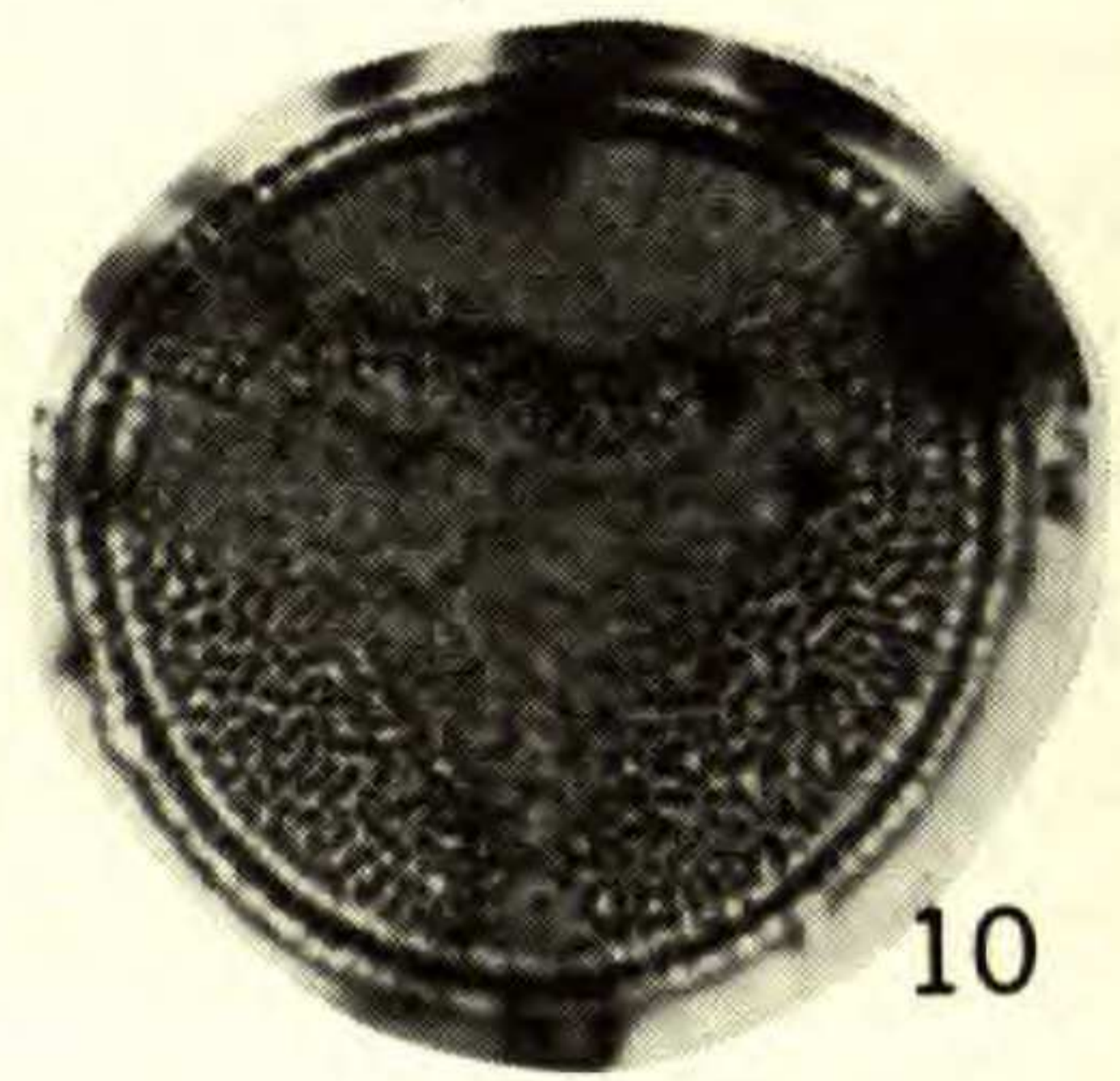
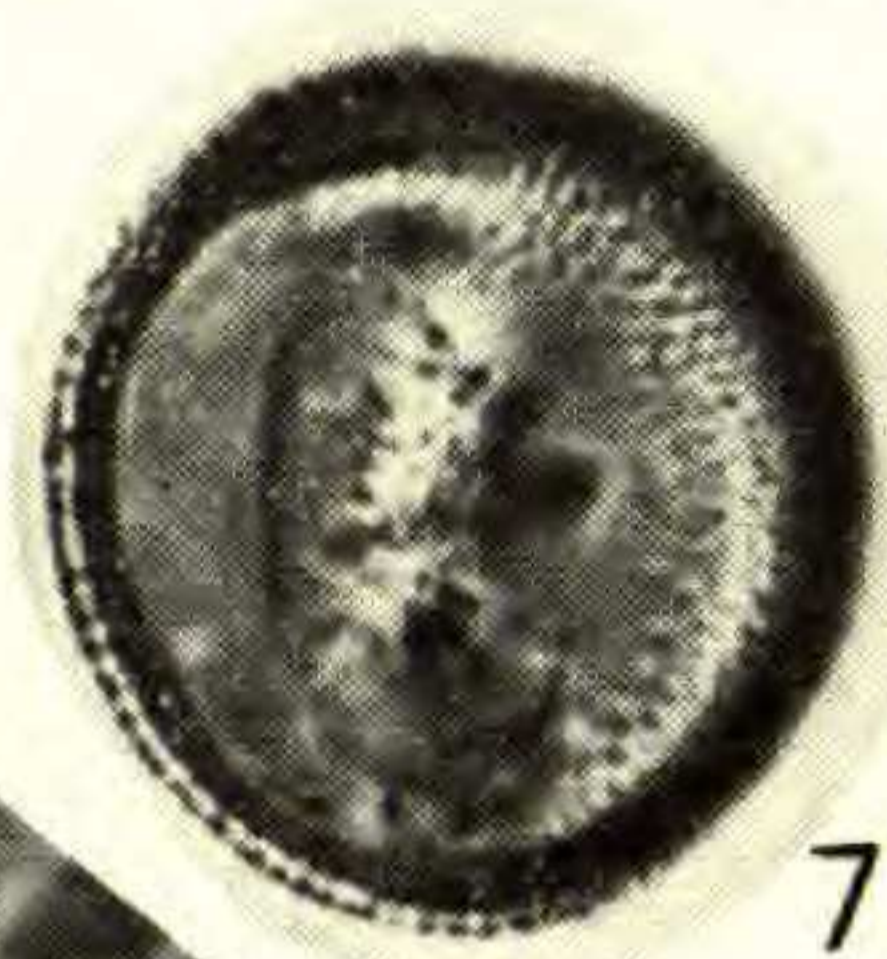
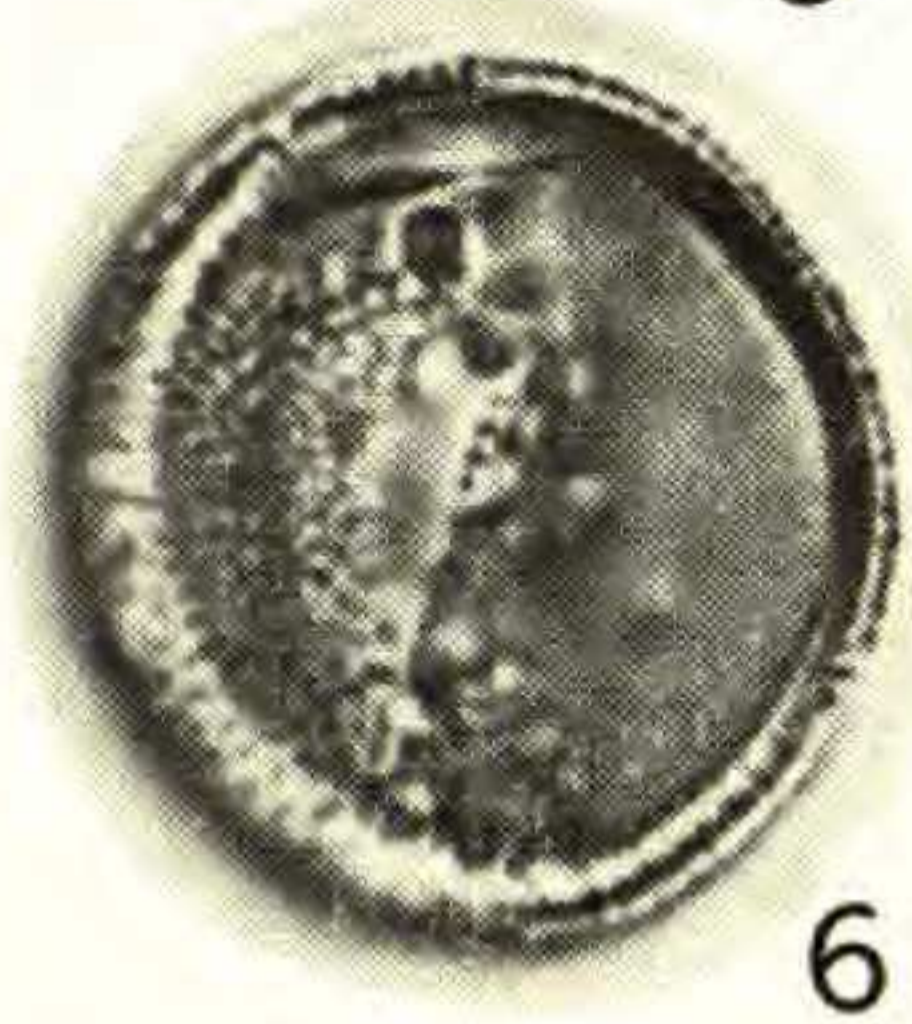
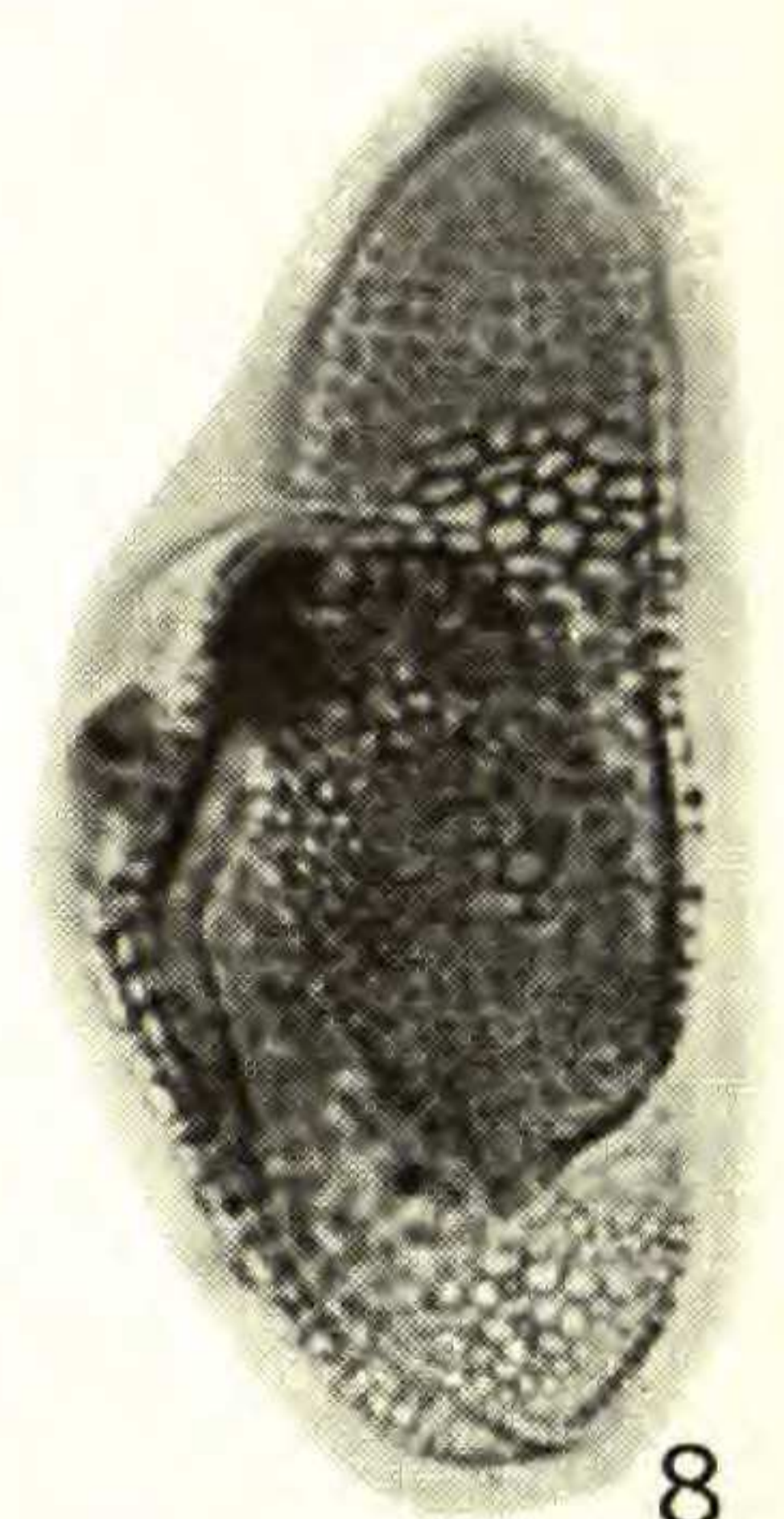
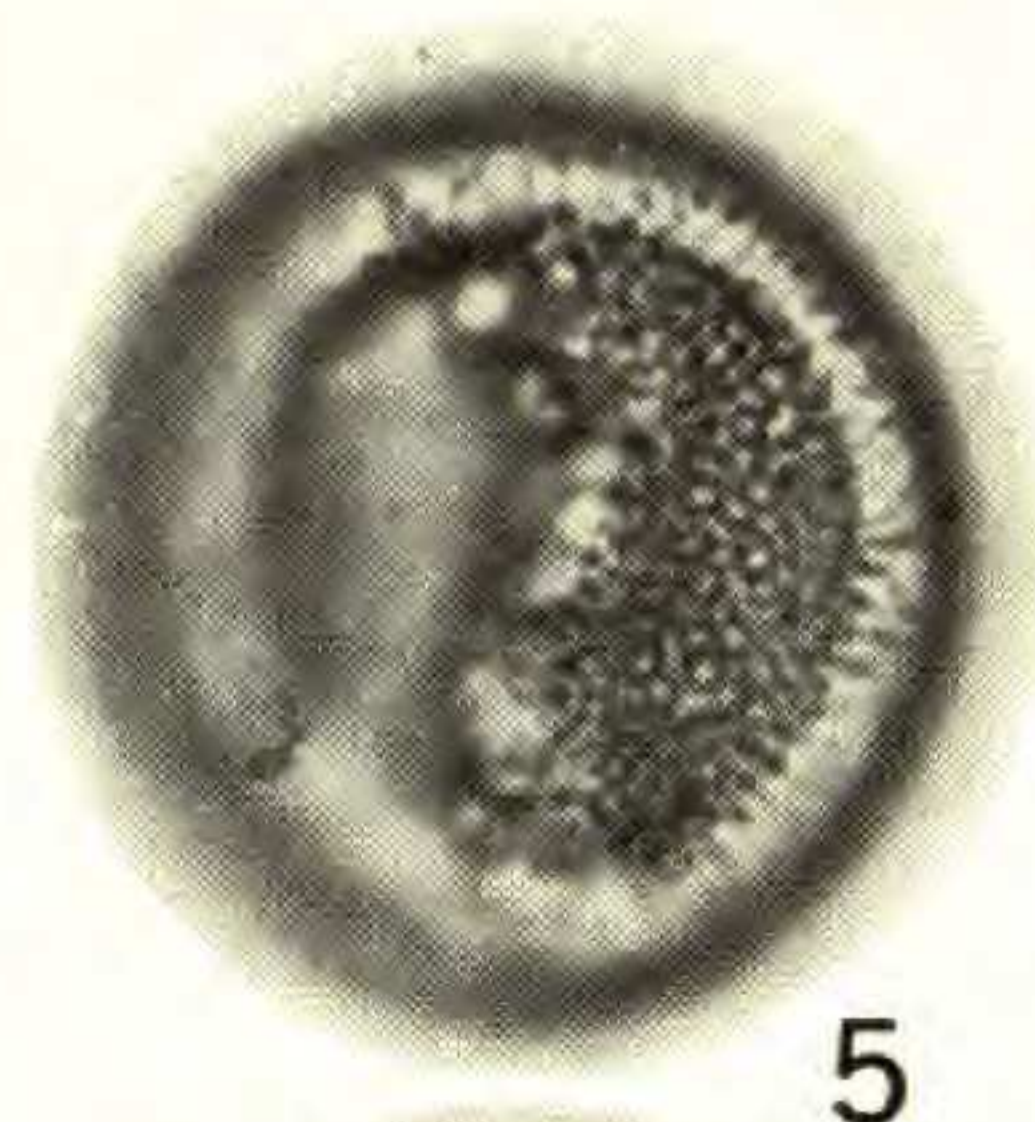
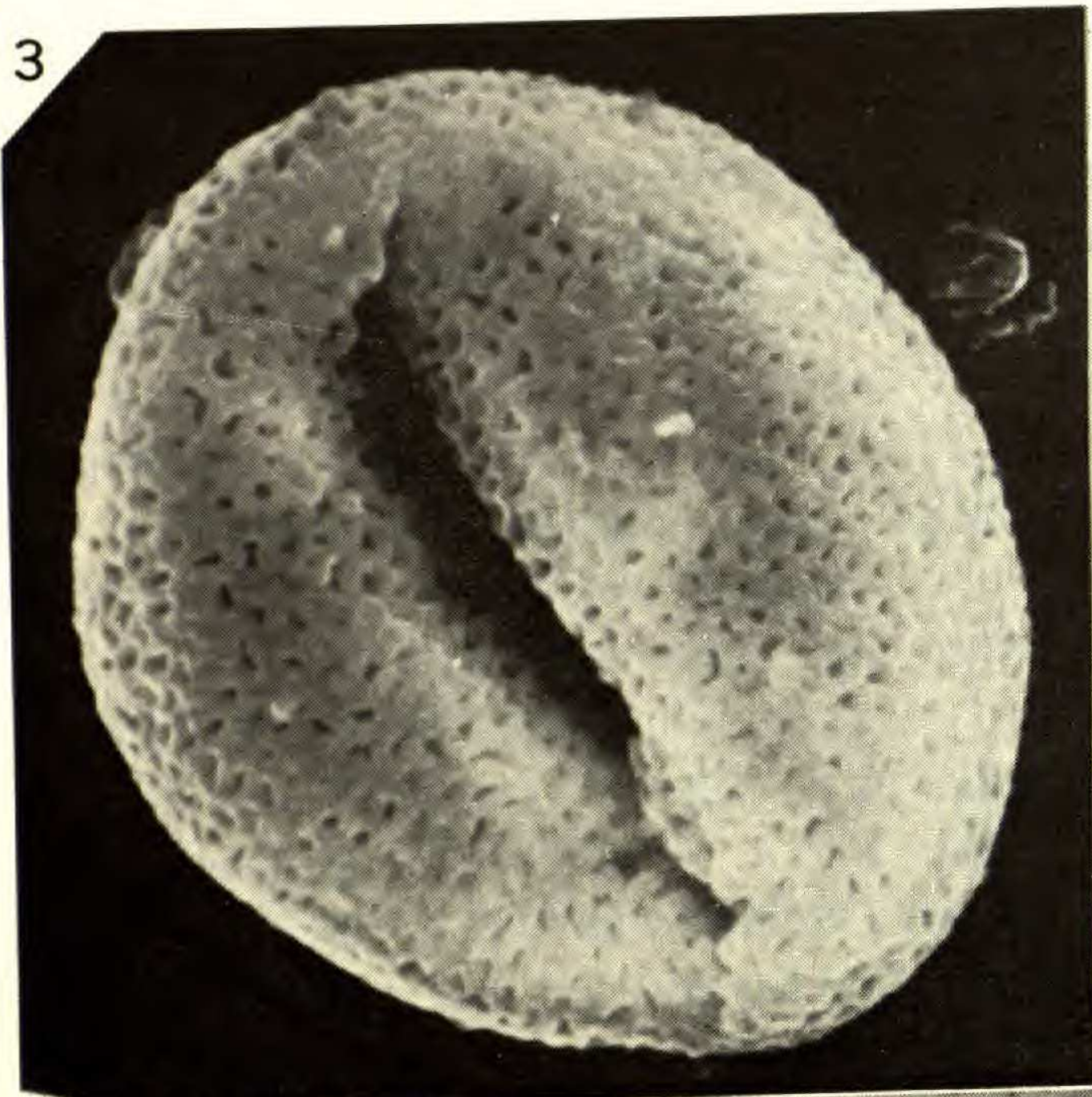
as a basis for conclusions on general questions of angiosperm phylogeny (Doyle, 1969a; Muller, 1970; Doyle & Hickey, in press).

The only angiospermous pollen grains in the lowest part of the Potomac Group (the lower half of Zone I of Brenner, 1963: Aptian?) are very subordinate monosulcate forms, with a single polar germination furrow, generally assigned to the form genera *Clavatipollenites*, *Retimonocolpites*, and *Liliacidites* (Figs. 3–9; cf. Brenner, 1963; Doyle, 1969a, 1970, 1973). Although monosulcate pollen also occurs in several groups of gymnosperms (e.g., Cycadales, Ginkgoales, Bennettitales), the above three genera have a wall or exine which is tectate and columellate, that is, consisting of an inner and outer layer (nexine and tectum) connected by a layer of well-defined rods or columellae (compare light and scanning electron micrographs of *Clavatipollenites*: Figs. 3–7), which is a character restricted to the angiosperms (Van Campo, 1971). Present SEM and light microscopic data indicate that exine structure of *Clavatipollenites* is tectate-perforate rather than clavate, as originally believed. This invalidates the “pilate or retipilate to reticulate or completely tegillate” trend postulated by Doyle (1969a: 28) and is more consistent with the tectate to semitectate to intectate trend of Walker (1974; Walker & Doyle, this symposium). *Clavatipollenites* (*C. hughesii*) was first described from presumably older (Barremian) rocks of England (Couper, 1958; Kemp, 1968), making it the oldest definite angiosperm pollen type known. Jurassic grains assigned to *Clavatipollenites* (cited by Muller, 1970) appear to have cycad-like alveolar exine structure and are hence not angiospermous. By early Potomac time, angiospermous monosulcates had already achieved some diversity, including larger, more coarsely reticulate, and suggestively monocotyledonoid forms (*Liliacidites*, with finer sculpture restricted to the ends of the grains and sulcus margins: Figs. 8–9; included in *Retimonocolpites* by Doyle, 1973).

In the upper part of Brenner's Zone I (lower Albian?), the monosulcates are joined by rare tectate-columellate tricolpate grains, with three longitudinal furrows or colpi (Figs. 11–13). Presumably somewhat older tricolpates are reported from Aptian rocks of Brazil (Müller, 1966), Africa (Jardiné & Magloire, 1965; Doyle, Jardiné & Doerenkamp, unpublished), and Israel (Brenner, in press). Although no actual transition is known, similarities in size and exine structure (compare Figs. 3–7 and 11–13) suggest that the earliest tricolpates were derived from the *Clavatipollenites-Retimonocolpites* complex. One of several hypotheses for the mode of origin of tricolpate pollen proposes that first the single polar furrow of monosulcate pollen developed into a three-armed structure (trichotomosulcate), and subsequently the central (polar) part of the furrow was eliminated, stranding the three arms as equatorially located colpi (Straka, 1963; Wilson, 1964). Though too young to be the actual intermediates, trichotomosulcate and irregularly colpate variants of *Clavatipollenites* are known from middle Zone II in the Potomac sequence (Fig. 10; Doyle, 1969a) and the middle Albian of Oklahoma (Hedlund & Norris, 1968).

Late Zone I and early Zone II tricolpates are relatively uniform in size, shape, and exine structure—small to medium-sized, prolate, and tectate to semitectate (reticulate)—but in the course of Zone II and Zone III (middle Albian through







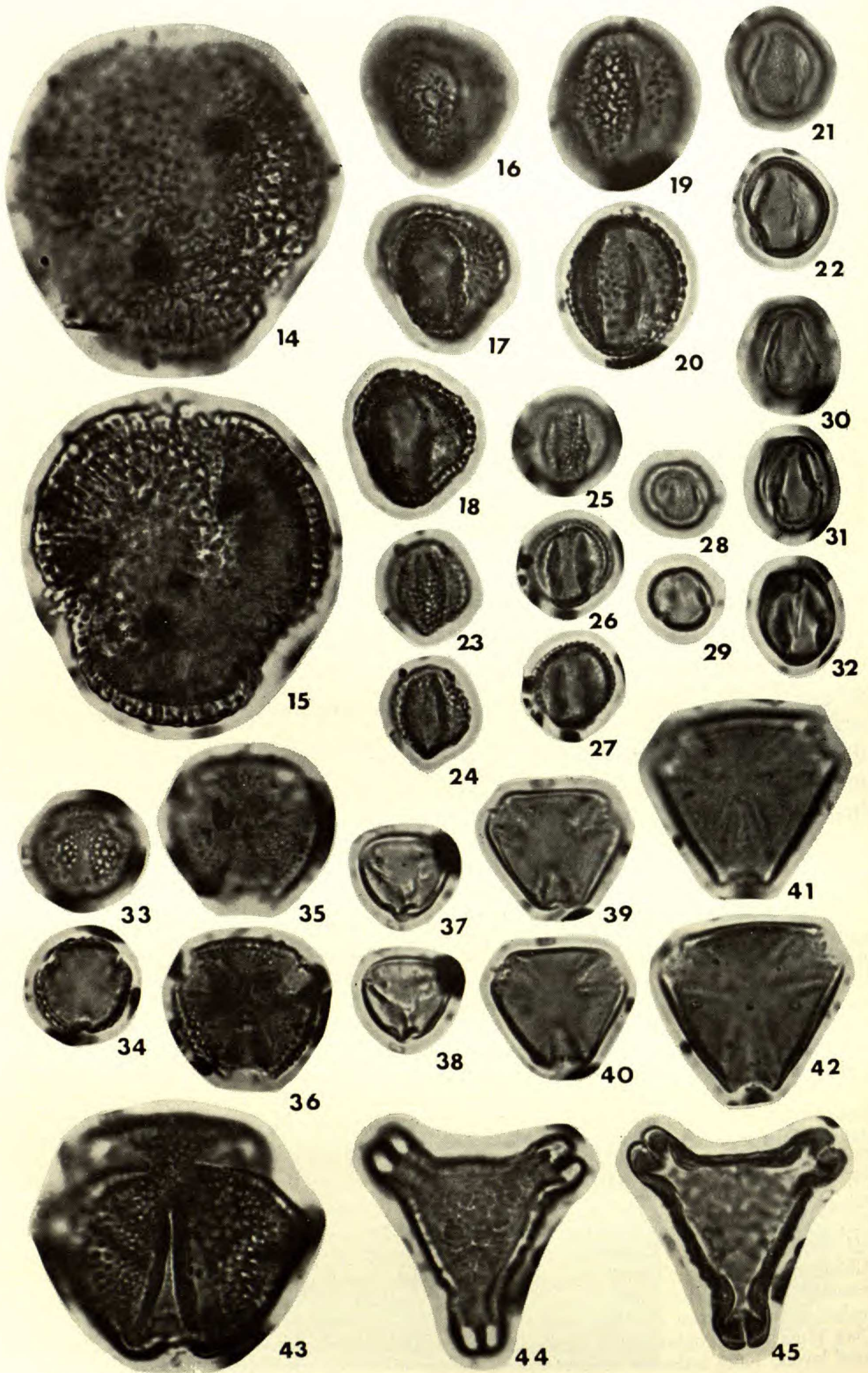
lower Cenomanian?) they undergo various independent and divergent modifications. Some of these involve size and sculpture, resulting in very large (Figs. 14–15), very small (Figs. 23–29), smooth-walled (Figs. 21–22), and coarsely sculptured, sometimes rugulate-reticulate grains (Figs. 16–20). Interestingly, many of the same trends are seen among contemporaneous monosulcates. A more significant trend, involving only the tricolpates, is the thinning of the colpus membranes and margins at the equator, culminating by Zone III times (lower Cenomanian?) in distinct ora associated with the colpi—the tricolporate condition (Figs. 25–40). Significantly, this trend apparently occurred independently in several tricolpate lines (as characterized on size and sculpture), although it is most common in the smaller and smoother lineages and is often correlated with a change in shape to oblate and triangular in polar view, with the apertures at the protruding corners of the grains (Figs. 37–42). Within Zone III and Zone IV (middle Cenomanian?), many of the tricolporates show a secondary tendency to increase in size and elaboration of exine structure and colpus margins (Figs. 33–43), a trend also inferred from comparative studies of modern tricolporate groups (Van Campo, 1966; Dahl, 1952). In at least one triangular tricolporate lineage, the shape modification trend is correlated with shortening of the colpi, leading to their elimination in the first triporate grains of Zone IV (Figs. 44–45). These grains represent early members of the Normapolles complex, a group which flourished during the Late Cretaceous in eastern North America and Europe (Góczán et al., 1967; Wolfe & Pakiser, 1971; Doyle, 1969a).

The evolutionary trends evidenced in the pollen of the Potomac-Raritan sequence and its equivalents have obvious phylogenetic implications if the successive transformations and grades of advancement are correlated with the distribution of characters in the modern flora. Here it is important to bear in mind that we are *not* using the systematic distribution of characters to establish first records of modern groups, but rather using the fossil record to draw con-

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FIGURES 3–13. Potomac Group (Cretaceous) angiosperm pollen: monosulcates and earliest tricolpates. All figures 1000× unless otherwise indicated; coordinates: UMMP Zeiss RA microscope # 4767359.—3–7. *Clavatipollenites* cf. *hughesii* Couper, 1958.—3. Lower Zone I (Aptian?). Angiospermous tectate-columellate monosulcate, scanning electron micrograph; ca. 4000×. Note well-developed tectum with numerous perforations. Sample Aq 27 (see Doyle, 1969a: 33).—4. Ca. 12,000×. Note occasional columellae visible through tectal perforations.—5–7. Light micrographs, three focal levels. Columellae appear as black dots at higher focal levels, radially oriented rods in optical section. Slide Aq 27-11, coordinates 7.4 × 85.2.—8–9. *Liliacidites* sp. (= *Retimonocolpites* sp. C, sensu Doyle, 1973), lower Zone I (Aptian?). Monocotyledonoid monosulcate, two grains, two focal levels. Note differentiation of the reticulate sculpture into finer and coarser areas (ends, middle of grain respectively). 71-8-1d (Trent's Reach, Va.: preparation from USNM 3215), coordinates 7.6 × 89.0.—10. Cf. *Asteropollis asteroides* Hedlund & Norris, 1968; middle Subzone II-B (upper middle Albian?). Trichotomosulcate variant of the *Clavatipollenites* complex. D12-520-2b (Delaware City well D12: Delaware Geological Survey well # Dc 53-7), coordinates 8.3 × 93.2.—11–13. Aff. "*Tricolpopollenites*" *crassimurus* Groot & Penny, 1960.—11. Upper Zone I (Aptian-lower Albian?). One of the oldest Potomac reticulate-tectate tricolpates (non-magnoliid dicotyledons), scanning electron micrograph; ca. 4000×. Note similarity of the tectate-perforate to reticulate sculpture to that seen in *Clavatipollenites* (Figs. 3–4). Sample 69-21 (Arundel Clay, United Clay Mine, near Poplar, Md.: Station 6 of Brenner, 1963).—12–13. Light micrographs, two focal levels. Note reticulate sculpture, columellae. 69-21-1a, coordinates 9.9 × 90.3.







clusions on the relative advancement of modern groups (or actually their most primitive members) and to evaluate proposed relationships between them. The first appearance of particular pollen types represent only *maximum* presently allowable ages of the modern groups that retain them; the vast majority of mid-Cretaceous pollen types are probably distant common ancestors of the various groups cited or extinct early side branches with no direct modern descendants, and not plants that could be assigned to modern families, orders, or even subclasses.

First, the oldest and presumably primitive monosulcate pollen type (as in *Clavatipollenites*, *Retimonocolpites*, and *Liliacidites*) is now restricted to the

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FIGURES 14–45. Potomac-Raritan (Cretaceous) angiosperm pollen, illustrating trends within the triaperturate complex. All figures 1000 $\times$ ; coordinates: UMMP Zeiss RA microscope # 4767359.—14–15. "*Retitricolpites*" *geranioides* (Couper) sensu Brenner, 1963; upper Subzone II-B (lower upper Albian?). Reticulate tricolpate, two focal levels. Note large size, coarse columellae. Slide D13-540-1b (Delaware City well D13: Delaware Geological Survey well # Ec 14-1), coordinates 18.2  $\times$  92.3.—16–18. "*Retitricolpites*" *vermimurus* Brenner, 1963; middle Subzone II-B (upper middle Albian?). Rugulate-reticulate tricolpate, three focal levels. Note coarse rugulate-reticulate sculpture. D12-515-1c, coordinates 13.0  $\times$  91.7.—19–20. Cf. "*Retitricolpites*" *georgensis* Brenner, 1963; middle Subzone II-B (upper middle Albian?). Reticulate tricolpate, two focal levels. Note coarse reticulate sculpture, especially in the mesocolpial areas. D12-590-1b, coordinates 7.1  $\times$  92.5.—21–22. *Tricolpites* cf. *albiensis* Kemp, 1968; middle Subzone II-B (upper middle Albian?). Tectate-psilate(?) tricolpate, two focal levels. Note very fine structure and nearly smooth exine. D12-515-1d, coordinates, 13.5  $\times$  99.4.—23–24. Aff. "*Tricolpopollenites*" *micromunus* Groot & Penny, 1960; Subzone II-A (lower middle Albian?). Reticulate tricolpate, two focal levels. Note small size, reticulate sculpture; compare with Figs. 25–27. D13-725-1a, coordinates 8.9  $\times$  91.3.—25–27. Aff. "*Tricolpopollenites*" *micromunus*, middle Subzone II-B (upper middle Albian?). Reticulate tricolporoidate, three focal levels. Compare with Figs. 23–24; note buckling-out of centers of the colpi. D13-600-1a, coordinates 5.3  $\times$  99.5.—28–29. "*Tricolpopollenites*" *minutus* Brenner, 1963; upper Subzone II-B (lower upper Albian?). Reticulate tricolporoidate, two focal levels. Note very small size, fine reticulate sculpture. D13-555-1b, coordinates 8.3  $\times$  98.6.—30–32. Cf. "*Tricolporopollenites*" *distinctus* Groot & Penny, 1960; Subzone II-C (uppermost Albian-basal Cenomanian?). Psilate tricolporoidate, three focal levels. Compare with Figs. 21–22; note small size, smooth exine, and oroid thin areas at the centers of the colpi. D13-420-1c, coordinates 9.7  $\times$  97.7.—33–34. *Tricolporodites* aff. *bohemicus* Pacltová, 1971; lower Zone III (lower Cenomanian?). Reticulate tricolporoidate, two focal levels. Compare with Figs. 35–36, 43. D12-275-1a, coordinates 3.2  $\times$  94.9.—35–36. *Tricolporopollenites* sp. A, upper Zone III (upper lower Cenomanian?). Reticulate tricolporate, two focal levels. Compare Figs. 33–34, 43; note larger size, more elaborated colpus margins than in Figs. 33–34. D13-215-1b, coordinates 15.4  $\times$  99.9.—37–38. Aff. "*Tricolporopollenites*" *triangulus* Groot et al., 1961; upper Subzone II-B (lower upper Albian?). Psilate tricolporoidate, two focal levels. Compare Figs. 39–42; note small size, smooth exine, and subtriangular equatorial outline. D13-555-1b, coordinates 6.1  $\times$  98.8.—39–40. *Tricolporopollenites* sp. B, lower Zone III (lower Cenomanian?). Psilate triangular tricolporate, two focal levels. Compare Figs. 37–38, 41–42; note larger size, more elaborated colpus margins, and more triangular shape than in Figs. 37–38. D13-335-1a, coordinates 15.6  $\times$  98.2.—41–42. *Tricolporopollenites* sp. C, Zone IV (upper lower-middle Cenomanian?). Psilate triangular tricolporate, two focal levels. Compare with Figs. 37–40; note larger size, thicker exine. 69-13-1d (clay lens in Farrington Sand member of the Raritan Formation, sand pit east of Mill Brook; New Brunswick, New Jersey, 7½-minute quadrangle), coordinates 19.6  $\times$  96.2.—43. *Tricolporopollenites* sp. D (= Tricolporate type 3 sensu Doyle, 1969a), Zone IV (upper lower-middle Cenomanian?). Reticulate tricolporate. Compare with Figs. 33–36; note larger size, thicker exine. 68-8-1a (see Doyle, 1969a: 34), coordinates 10.4  $\times$  102.3.—44–45. *Complexiopollis* sp., Zone IV (lower upper Cenomanian?). Early member of the triplicate Normapolles complex, two focal levels. NJ 2-1b (see Doyle, 1969a: 34), coordinates 8.2  $\times$  103.9.



monocotyledons and to the subclass Magnoliidae (sensu stricto of Takhtajan, 1969) in the dicotyledons (cf. Walker & Doyle, this symposium). *Clavatipollenites* and *Retimonocolpites* are too generalized to determine whether they were produced by monocotyledons or primitive dicotyledons, but *Liliacidites*, which extends down to the base of the Potomac sequence (Figs. 8–9), has a sculpture pattern (coarsely reticulate on most of the grain, finely reticulate at the ends and/or sulcus margins) that is now restricted to the monocotyledons (Doyle, 1973). Second, triaperturate pollen is restricted to, and apparently basic to, the six dicotyledonous subclasses other than Magnoliidae (Ranunculidae, Hamamelididae, Caryophyllidae, Dilleniidae, Rosidae, and Asteridae; cf. Walker & Doyle, this symposium). Relatively primitive reticulate tricolpate pollen is retained by many Ranunculidae, “lower” Hamamelididae (e.g., Trochodendrales, Hamamelidales) and Caryophyllidae, and a few Dilleniidae (Dilleniaceae), although it is of course unlikely that the first tricolpates would be assignable to any of these relictual and divergently specialized modern tricolpate taxa. The more advanced tricolporate condition is found in a few Ranunculidae (e.g., some Menispermaceae), Hamamelididae (e.g., Fagaceae), Caryophyllidae (e.g., Polygonaceae), and appears to be basic to Rosidae, Asteridae, and Dilleniidae exclusive of Dilleniaceae. Successive stages in the size and structure elaboration trends seen in Zones III and IV are preserved within modern tricolporate alliances: the more primitive, small, smooth type is seen in Cunoniaceae and many other Saxifragales in the Rosidae, and in Theaceae-Ternstroemioidae, Ochnaceae, Flacourtiaceae, and Elaeocarpaceae in the Dilleniidae, while most other families in the same subclasses (e.g., Rutaceae, Nyssaceae, Celastraceae, Rhamnaceae, Theaceae-Camellioideae, Tiliaceae, etc.) have larger, structurally more elaborated forms (cf. Walker & Doyle, this symposium). Finally, the advanced triporate pollen type is prevalent among many of the classic “Amentiferae” or higher Hamamelididae (Betulaceae, Myricaceae, Casuarinaceae, Rhoipteleaceae, Juglandaceae, Urticales), though forms showing the specializations of modern amentiferous families and orders do not become differentiated until near the end of the Late Cretaceous (Wolfe, 1973).

These broad conclusions on the relative advancement of groups are generally consistent with so-called “ranalean” theories of angiosperm evolution (such as form the basis of the Takhtajan and Cronquist systems), and clearly contradict theories that the “Amentiferae” are relatively primitive within the angiosperms. More direct inferences on the phylogenetic relationships of major modern groups are possible if we consider the evidence for single versus multiple origin of specific pollen characters. On the one hand, all the triaperturate types in the Potomac-Raritan sequence can be traced back into a morphologically generalized complex of tectate-reticulate tricolpates. Hence, although the existence of so many parallel trends involving size and sculpture in both monosulcate and triaperturate groups makes us wary of other parallelisms, the Potomac evidence is consistent with a single origin of the tricolpate condition and hence the hypothesis that the six non-magnoliid dicotyledonous subclasses form a monophyletic group. Because no modern families (except Nymphaeaceae sensu lato) or even orders or subclasses in the system of Takhtajan (1969) include both monosulcate and tricolpate



members, this possibility is consistent with comparative evidence. However, this question cannot be considered resolved until detailed investigations of sequences in other areas reveal actual intermediates in the origin of tricolpates. On the other hand, the fossil evidence clearly indicates that the tricolporate condition arose independently in many tricolpate lineages. Hence modern tricolporates form a highly polyphyletic assemblage, as the coexistence of tricolpates and tricolporates in many alliances would indicate (cf. Walker & Doyle, this symposium; and above).

The inferred evolutionary sequence from tricolpates through triangular tricolporates to triporates of the Normapolles type also raises doubts concerning the proposed close relationship (Cronquist, 1968; Takhtajan, 1969) of the triporate "Amentiferae," or higher Hamamelididae, to the Hamamelidales. In the later Upper Cretaceous, certain lineages of the Normapolles complex grade morphologically into pollen assignable to the Juglandales (Wolfe, 1973), and other higher Hamamelididae have also been considered as Normapolles derivatives (Góczán et al., 1967; Doyle, 1969a). The closest relatives of the higher Hamamelididae should thus be sought among groups with triangular tricolporate pollen, such as primitive Rosidae (e.g., Cunoniaceae), rather than among Hamamelidales, which have reticulate tricolpate pollen. Such a suggestion is consistent with interpretations of the foliar morphology of Juglandales (Wolfe, 1973; Hickey & Wolfe, this symposium), which indicate that they are allied to Rosidae. We thus raise the question as to whether Rosidae and Hamamelididae are as unrelated as assumed in the Takhtajan/Cronquist systems.

Many phylogenetic implications of the later Cretaceous and Tertiary pollen record, especially as related to the first appearances of pollen types assignable to particular modern families, are discussed by Muller (1970). Here we will cite only the appearance of distinctive pollen types allied to palms (and palm megafossils: cf. Read & Hickey, 1972; Doyle, 1973) late in the Upper Cretaceous (Senonian), of graminoid pollen near the Cretaceous-Tertiary boundary (cf. Jardiné & Magloire, 1965), and of pollen of many characteristically herbaceous dicotyledonous families in the middle to late Tertiary (e.g., Compositae, Acanthaceae, Labiatae).

#### LEAVES

Recent reinvestigations of mid-Cretaceous leaves, although less complete than the pollen studies, have contradicted early attempts at systematic identification (e.g., Fontaine, 1889; Berry, 1911) and the resulting concept of a highly differentiated Cretaceous angiosperm flora (Pacltová, 1961; Wolfe, 1972), and in fact reveal a pattern of increasing morphological diversity similar to that seen in the pollen record (Doyle & Hickey, 1972, in press; Hickey & Doyle, 1972).

In the Potomac Group, Zone I leaves (Aptian-lower Albian?) include both an apparently herbaceous monocotyledon (Doyle, 1973) and a limited diversity of simple, pinnately veined dicotyledons (Doyle & Hickey, 1972, in press; Wolfe, 1972). The irregularity in course of the secondary veins and the poor differentiation of vein orders correspond to the "first rank" venation pattern, which Hickey (1971) had concluded on the basis of comparative studies is the primitive condition in the dicotyledons (cf. Hickey & Doyle, 1972). The joint occurrence



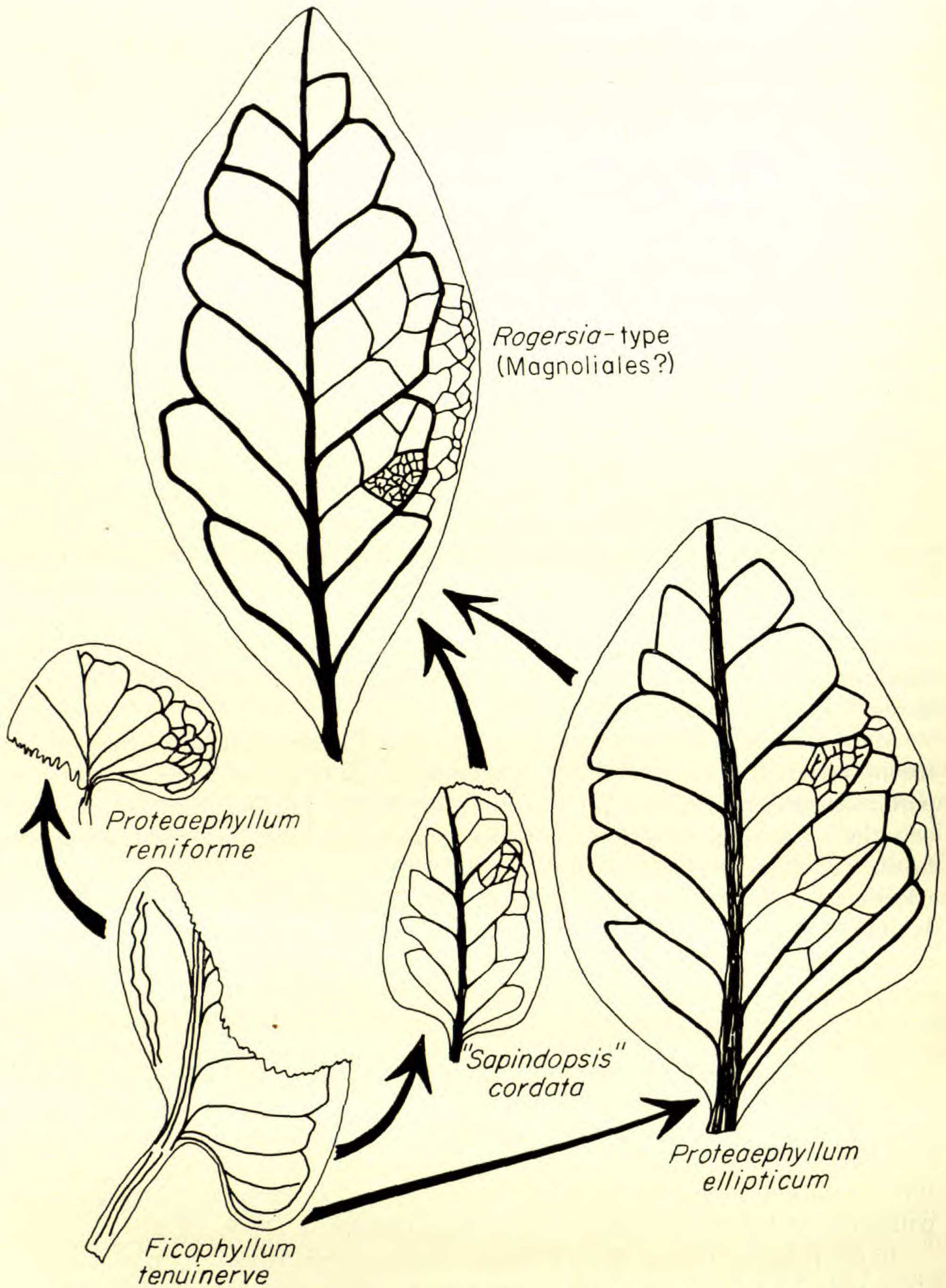


FIGURE 46. Suggested phylogeny of morphological types represented by dicotyledonous leaves from the Fredericksburg locality (lower? Albian) of the Patuxent Formation, Virginia.



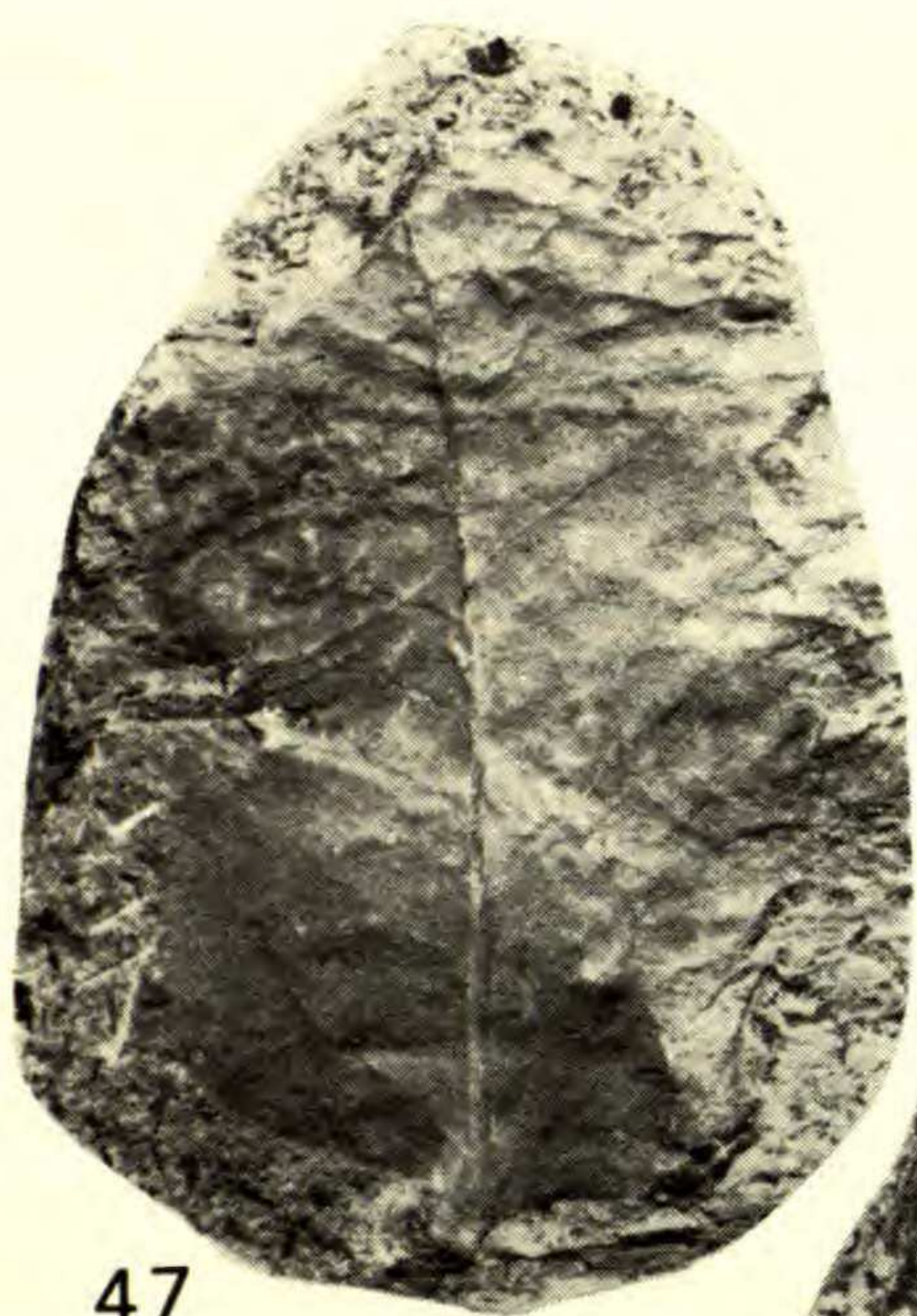
of foliage of this type with tectate-columellate monosulcate pollen, moreover, is an indication that at least some of this pollen was produced by dicotyledons.

The most prolific locality for early Potomac leaves is Fontaine's locality at Fredericksburg, Virginia (upper Zone I: lower Albian?), where approximately ten species of dicotyledons are represented. Although all are coeval, they can be interpreted as a morphological series (Fig. 46); it might be expected that intermediate forms as well as the older and younger would be present in the same assemblage if we are witnessing the initial radiation of the dicotyledons. The most poorly organized type is that called *Ficophyllum tenuinerve* (Fig. 50): the midrib is composed of at least three discrete strands, and the thin, decurrent secondary veins diverge at highly variable angles to loop weakly and irregularly well within the margin. The intercostal venation is poorly developed, lacks obvious tertiary bracing and could not have given much structural support to the lamina. From such a type, which is decidedly reniform, it would be a short step to *Proteaephyllum reniforme* (Fig. 51), which has a stronger series of loops and a more pronounced intercostal venation; *P. reniforme* also shows a tendency toward a palmately veined condition (actinodromy), and it is tempting to suggest that actinodromous leaves found higher in the Potomac section represent a continuation of this trend (Doyle & Hickey, in press).

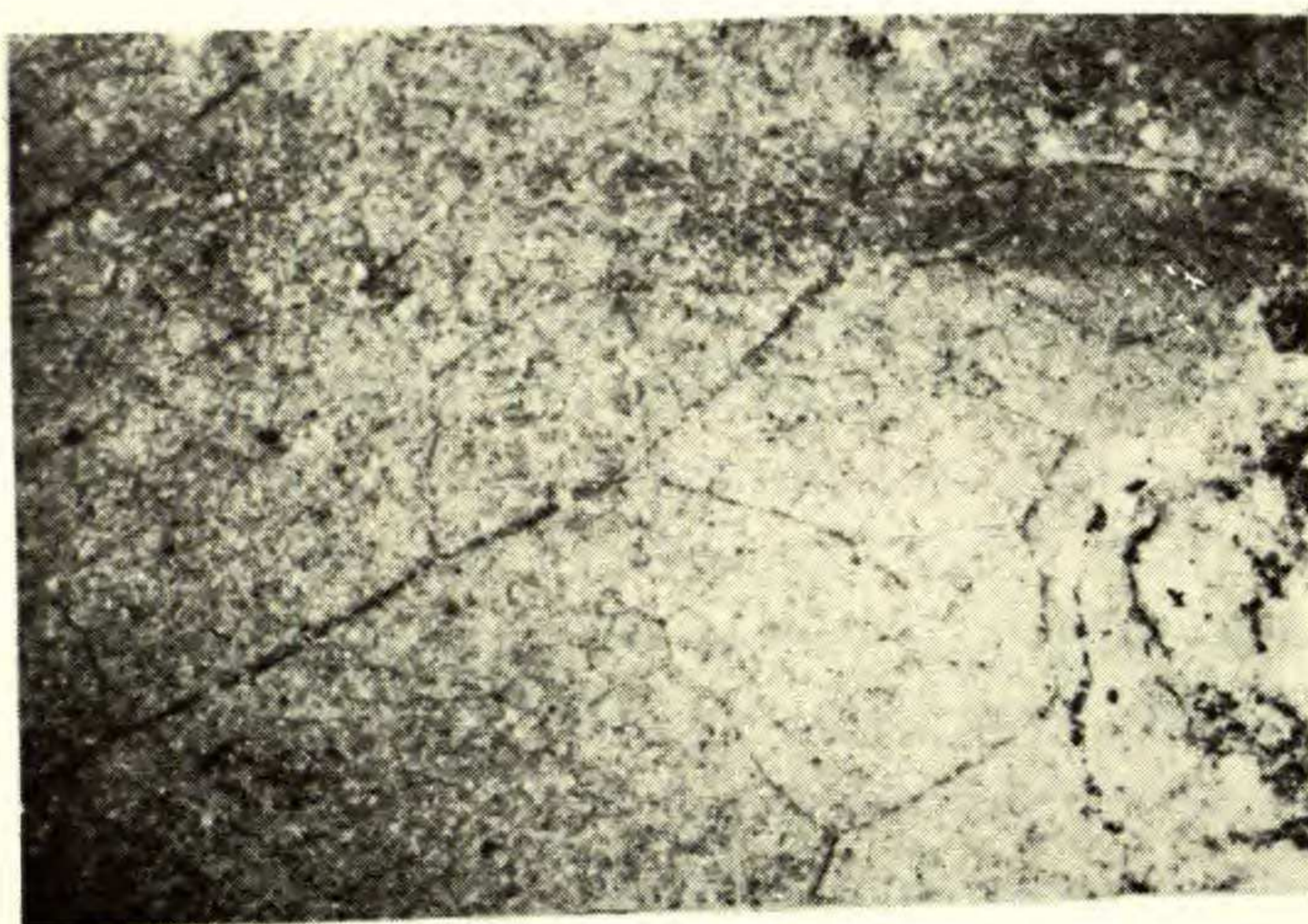
Probably the more significant trend is that represented by *Proteaephyllum ellipticum* (Fig. 49) and "*Sapindopsis*" *cordata* (Figs. 47–48; not to be confused with the type of *Sapindopsis* mentioned later). In these forms, the midrib is, except near the base, organized into one thick strand. The angles of divergence of the secondary veins are more uniform, and the secondaries are supported by thin but definite tertiary braces. A fourth order of venation is also present. Although still having a broad base, these forms are not peltate. The most highly organized forms represent at least four species, variously referred to *Ficophyllum*, *Ficus*, *Salix*, and *Rogersia* (Figs. 52–53). The *Rogersia* type clearly has a reticulation more consistent in shape and size than these other forms, and the widest part of the lamina is at or above the middle. To these four forms—all of which are entire-margined—can be added two toothed forms that have the same basic venation type. The teeth are, however, unusual in having no glands and in that the veins do not reach the outermost part of the tooth. Comparison with leaves of extant dicotyledons indicates that the more organized leaves at Fredericksburg correspond to a grade represented today only in the Magnoliidae and particularly in the Magnoliales (e.g., Winteraceae, Himantandraceae, and Canellaceae, although it is unlikely that the fossils represent any of these extant families). The grades represented by other Fredericksburg forms are even more disorganized and may indicate the existence of more primitive dicotyledons than any now extant.

Also present in the Fredericksburg dicotyledonous assemblage is the leaf called *Eucalyptophyllum* (Fig. 54). Although the venation is closed by an intramarginal vein as in many extant dicotyledonous groups (e.g., Myrtales, Ochnaceae, Dioncophyllaceae, Myrsinaceae), the intercostal venation is classed as Hickey's first rank. That is, the gross architecture is basically different from Magnoliales but the morphological grade is just as low as in many members of Magnoliales or other Fredericksburg dicotyledons. Such a leaf could well





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represent an extinct line that attempted organization of the venation in a basically different fashion than in the magnolialian line (Wolfe, 1972). Such pronounced examples of morphological experimentation make dubious any attempts to assign other early angiosperms to extant families or even orders.

Higher in the Potomac sequence (Subzones II-B and II-C of Zone II: middle and upper Albian?), dicotyledonous leaves become progressively more diverse in shape and venation patterns, including peltate, ovate-cordate, and variously lobate forms (Doyle & Hickey, 1972, in press). Within this interval, several lines achieve first "second rank" (with secondary veins regular in course and spacing), then "third rank" venation (with regularly oriented, percurrent tertiary veins; Hickey & Doyle, 1972).

One of the most conspicuous lower Subzone II-B leaf types is the pinnatifid genus *Sapindopsis*. In these leaves, the venation is still disorganized as in the magnolialian grade leaves at Fredericksburg, but the lamina is deeply dissected. Indeed, the more basal segments could properly be called leaflets, but the apical segments are continuously joined. The apical segment, moreover, typically has two strong veins entering the lobes. Higher in Subzone II-B are specimens of *Sapindopsis* that are truly pinnately compound (Doyle & Hickey, in press); that the pinnatifid and compound leaves are related is indicated both by similarities in venation and Mersky's (1973, and unpublished) studies of the cuticles, which demonstrate similar epidermal patterns. Correlative beds in Kansas and Kazakhstan have yielded pinnately compound *Sapindopsis* specimens that are toothed (*Sapindopsis belviderensis* Berry, 1922; "*Anacardites*" *neuburgae* Vakhrameev, 1952); the veins entering the teeth first bifurcate, sending one branch to the sinus and the other branch along the apical side of the tooth (Doyle & Hickey, in press). In terms of extant plants, such a relationship between teeth and venation is restricted to members of Rosidae (and derivative Asteridae), in which the pinnately compound condition is also prevalent (Wolfe, 1973; Hickey & Wolfe, this symposium). These species of *Sapindopsis* in the late Albian had reached the grade of foliar morphology characteristic of Rosidae, and we suggest that this series mirrors the evolution of Rosidae from dicots at a magnoliid evolutionary grade.

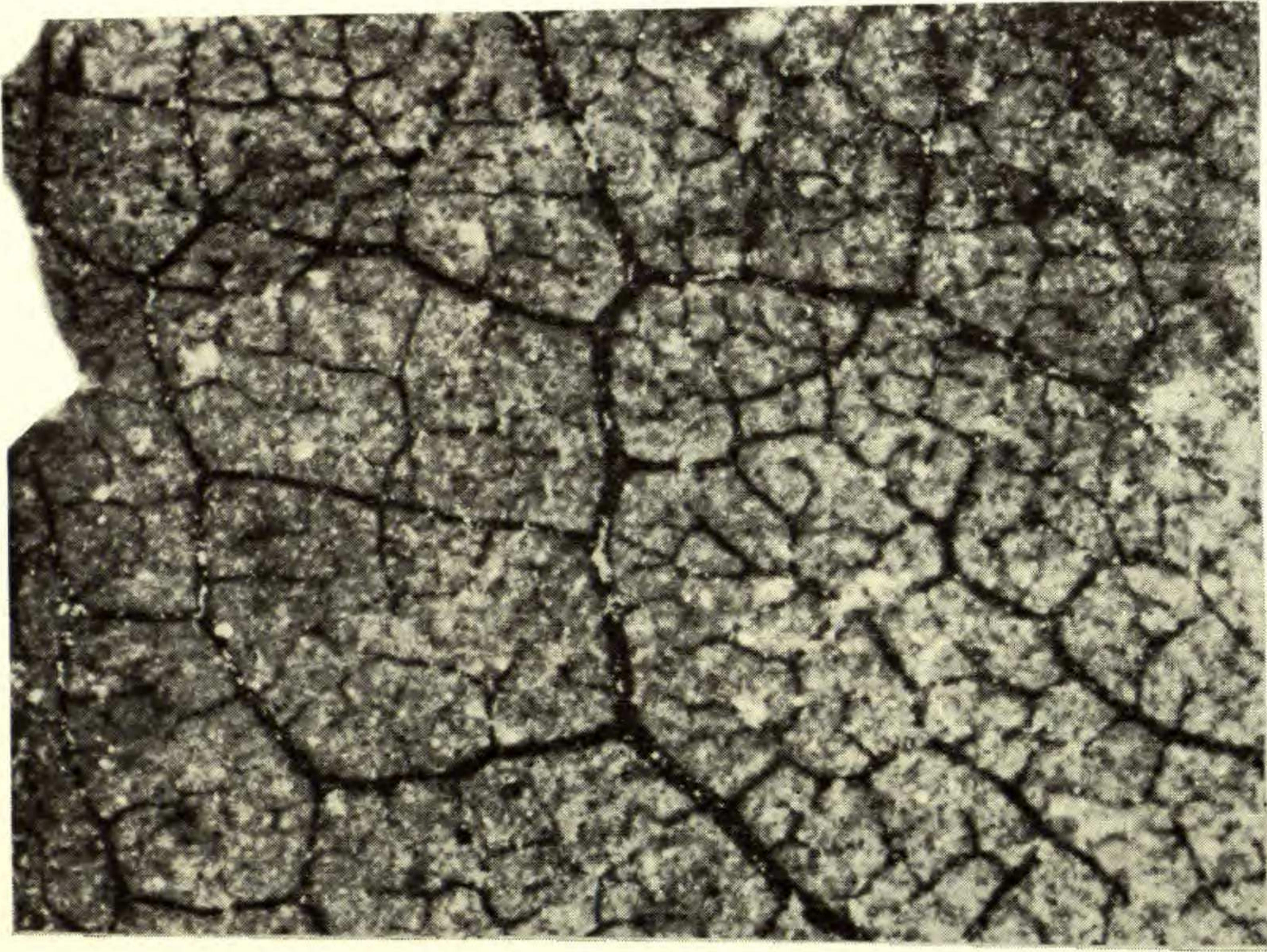
#### WOODS

One of the major evidences cited for a pre-Cretaceous diversification of angiosperms is the putative diversity and high morphological grade of vesselled woods described by Stopes (1913, 1915) and attributed to the Lower Greensand (Aptian) of England. As in early descriptions of Lower Cretaceous leaves, some of the Lower Greensand woods have been assigned to extant families (Theaceae, Dipterocarpaceae) that are at least moderately advanced in the systems of Cronquist and Takhtajan.

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 FIGURES 47–51. Dicotyledonous leaves from the Fredericksburg locality (lower? Albian) of the Patuxent Formation, Virginia.—47–48. "*Sapindopsis*" *cordata* Font., USNM 3229a.—49. *Proteaephyllum ellipticum* Font., USNM 3267.—50. *Ficophyllum tenuinerve* Font., USNM 3229a.—51. *Proteaephyllum reniforme* Font., USNM 3915.





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The geologic horizons from which Stope's (1913, 1915) woods were actually derived have been validly questioned by some workers (e.g., Hughes, 1961; Harris cited in Casey, 1961). The doubts concerning the derivation are based on the fact that (1) the specimens were separately collected, deposited in local museums, and years later transferred to the British Museum, where Stopes first examined them, (2) the locality labels accompanying the specimens are vague (e.g., the specimen of *Hythia* reads: specimen presented by the Committee of the Maidstone Museum, date of collection and precise locality unknown), and (3) despite extensive geologic investigations of the Lower Greensand since 1915, no angiosperm wood has been recovered. On the other hand, Casey (1961) stated that the matrix of three of the specimens (*Hythia*, *Aptiana*, *Cantia*) matched well the lithology of the Lower Greensand (the other two specimens lack matrix), thus offering some support for the supposed age of these three specimens. One of the woods having matrix, *Cantia*, is supposedly from the Folkestone Beds at the top of the Lower Greensand and is thus of early Albian rather than Aptian age.

The two specimens—those of *Woburnia* and *Sabulia*—that lack matrix are, interestingly, the structurally most specialized (under current concepts in comparative anatomy) of the Lower Greensand woods. We suggest that these two woods are of highly questionable derivation and further consideration of them is valueless. The remaining three woods, because they may in fact have been collected from the Lower Greensand, are worthy of attention.

The wood called *Hythia* is apparently the oldest of the three (early part of the late Aptian). Interpretations of structure in this specimen are made difficult by the poor lignification of the cell walls, which led Stopes (1915) to conclude that the wood was originally "very soft." In some features (e.g., large pores or vessels), the wood is specialized, but in other features (e.g., solitary pores, scalariform perforation plates, apparently heterogeneous rays, diffuse parenchyma) it is not particularly advanced.

Even less specialized is the latest Aptian *Aptiana*. The solitary pores are only half again as large as the fibers in cross section; the rays are heterogeneous and are composed of large, square and upright cells in radial section and the multi-seriate rays have long, uniseriate margins of upright cells. On both radial and tangential walls of the fibers, bordered pits occur in uniseriate or biseriate rows. The type of pitting in the vessels is not certain but the vessels may have scalariform perforation plates. The parenchyma is diffuse. This morphological grade can be found today among the putatively primitive families of all major groups of dicotyledons and could be regarded as advanced only in possessing vessels, i.e., this pattern is only one morphological grade higher than the vesselless condition.

The lower Albian *Cantia* is possibly somewhat more specialized, but the small

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FIGURES 52–54. Dicotyledonous leaves from the Fredericksburg locality (lower? Albian) of the Patuxent Formation, Virginia.—52. "*Sapindopsis*" *elliptica* Font., USNM 3261 (*Rogersia* type).—53. *Rogersia angustifolia* Font., USNM 3236a.—54. *Eucalyptophyllum oblongifolium* Font., USNM 3273.



solitary pores, square and upright ray cells, and scalariform perforation plates are unspecialized features. None of these three woods has wood patterns more specialized than patterns found in advanced members of Magnoliidae. We suggest that these three woods are consistent with our interpretations of the pollen and leaf record, that is, there is no evidence that these woods represent a morphological grade more advanced than that now found in Magnoliidae. On the other hand, we also emphasize that until such time as vesselless dicotyledonous woods have been recovered with certainty from the Lower Greensand, the evolutionary significance of Stopes's woods should be viewed with caution.

An Aptian wood of known provenance and possible angiospermous affinities is known from Japan (Nishida, 1962). This homoxyle wood has many similarities to the wood of vesselless dicotyledons such as *Tetracentron* and was assigned without qualification to the dicotyledons by Nishida. While the assignment of Nishida's wood to the dicotyledons would lend support to a Cretaceous origin and diversification of the angiosperms, we emphasize that there are some doubts as to the validity of this assignment. The fossil, which has pitting on the tangential as well as the radial walls, contrasts with extant vesselless angiosperms in which scalariform pitting occurs only on the radial walls of tracheids. The fossil also has disorganized multiseriate rays; in similar extant woods, the rays have a definite pattern of organization except typically near the departure of a branch. Indeed, rays typically become both enlarged and disorganized in such regions, and it is possible that the fossil, in which multiseriate rays are described as being rare, came from a stem that was typically uniseriate; the uniseriate condition is unusual in extant vesselless dicotyledons.

Thus, of the three putative dicotyledonous woods of Aptian age, one is vesselless and one is of an apparently very primitive vesselless type. Certainly more information is needed to establish trends and levels of advancement in the woods of the early angiosperms; only with such information can concepts of phylogeny and concepts of the relative primitiveness of anatomical features be properly evaluated.

Other reports of reliably dated and well documented Cretaceous dicotyledonous woods are, unfortunately, rare. One assemblage of 70 entities from the late Campanian or early Maestrichtian of California (Page, 1967, 1968, 1970, and unpublished) and a second assemblage of five entities from the Maestrichtian of Illinois (Lawrence Matten, unpublished) tend to substantiate that the supposedly advanced anatomical features are, in fact, geologically more recent than supposedly primitive features. Over half these wood patterns have solitary pores or solitary with a few short radial chains, and the majority also have diffuse axial parenchyma only (the remainder have some vasicentric parenchyma in addition). Similarly, scalariform perforation plates are found in the majority and the rays are heterogeneous in almost all these woods. Two of the entities are dicotyledons lacking vessels. Some of the woods do have some specialized elements, such as short vessels and aggregate rays, but the overall pattern of these woods is not advanced. None of the woods possess supposedly advanced features such as storied elements, included phloem, aliform or confluent parenchyma, or elaborate pore distribution. Although many of the specimens may represent young stems



in which the mature patterns might have been more specialized, we think that it is highly significant that as late as the Maestrichtian, wood patterns had apparently reached only a moderate level of specialization.

Patterns at the same grade of specialization as those encountered in about half of Matten's and Page's woods occur today in less than 30% of the families of woody dicotyledons. That is not to say that all members of these families have this same grade, because many members may have much more specialized patterns. Aside from members of Magnoliidae, such less specialized patterns occur in the supposedly more primitive members of Dilleniidae (e.g., Dilleniaceae, Theaceae, Flacourtiaceae, Symplocaceae, Saurauiaceae, Daphniphyllaceae, Dichapetalaceae), less frequently in the Rosidae (e.g., Cunoniaceae, Hydrangeaceae, Aquifoliaceae, Cornaceae), Hamamelididae (e.g., Cercidiphyllaceae, Eupteleaceae, Hamamelidaceae, Myricaceae), and only in one family of Asteridae (Caprifoliaceae). Indeed, some of the California woods are considered to be allied to Magnoliales, Laurales, Trochodendrales, Ranunculales, Hamamelidales, and Saxifragales (Page, 1967, 1968, 1970).

#### POST-CRETACEOUS DIVERSIFICATION

That major angiosperm diversification continued following the Cretaceous is indicated by a taxonomic analysis of the London Clay flora, an early Eocene assemblage based on fructifications. Comparing this assemblage of about 350 dicotyledonous species with the vegetationally comparable flora of lowland Taiwan (471 species), it can be seen that specific diversity within Magnoliidae has drastically declined since the Eocene. In the London Clay flora, fully 25% of the species belong to Magnoliidae, whereas only 8% of the Taiwan species fall into this subclass. More significantly, whereas the lowland flora of Taiwan has representatives of 14 families of woody Asteridae, the London Clay contains but four, and notably lacking are Asclepiadaceae, Rubiaceae, and Verbenaceae. At the generic level, the London Clay flora contains but six members of Asteridae, in contrast to the 54 represented in lowland Taiwan. Such comparisons are consistent with the well-known first appearance of presumed advanced Asteridae, such as Compositae, near the Oligocene-Miocene boundary. Clearly, paleobotanical work to assist in the unraveling of the phylogeny of the angiosperms at higher taxonomic levels will involve work not just in the Cretaceous but also in the Tertiary (cf. Muller, 1970).

#### CONCLUSIONS

This report has, we hope, shown both the potential value of paleobotany to interpretations of phylogenetic relationships among extant angiosperms and the need for much additional work on the paleobotany of the angiosperms. Specifically, paleobotany strongly supports the primitiveness of Magnoliidae relative to the other subclasses of the dicotyledons. The evidence also indicates that the split between the monocots and dicots occurred early and prior to either class having attained even a moderate level of advancement. The earliest tricolpate pollen is small and finely sculptured, the same type that occurs in putatively primitive members of Hamamelididae and in the Ranunculidae; the geologically



younger and derived tricolporate grade is basic to subclasses Rosidae, Asteridae, and Dilleniidae (except Dilleniaceae). The pollen type possessed by the higher Hamamelididae or Amentiferae, p.p., and the Rosidae is younger geologically than the type possessed by putative ancestors. Fossil foliage provides a gradational series from a type now characteristic of Magnoliales to a type basic to Rosidae. The evidence may indicate, however, that Hamamelididae and Rosidae are more closely related than the Takhtajan-Cronquist system suggests. Our interpretations of the Early Cretaceous pollen and leaf records indicate that the evolutionary rates were comparable, i.e., both leaf and pollen records display an increasingly higher level of morphological complexity in the same sequence. We also suggest that as studies in critical areas, both geographically and geologically, are carried out, paleobotany will make an increasingly significant contribution to an understanding of the phylogeny and classification of the angiosperms.

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